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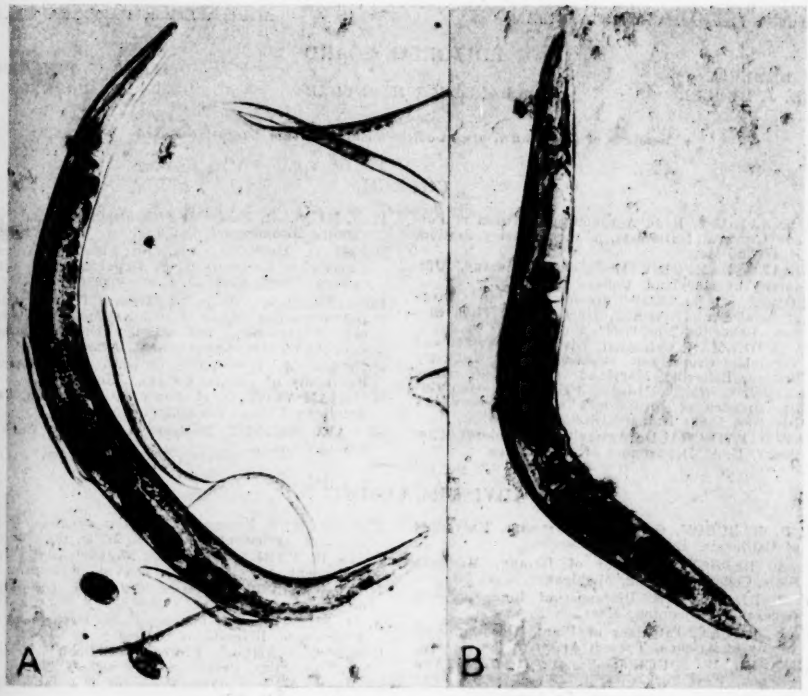

DWARF MUTANT NEMATODE
(SEE PAGE 103)

Dimorphic Fruit Shape in Squash

How Genetics Illuminates Evolution

Polyembryony and Haploidy in Peppers

X-Rays Do Not Resuscitate Heat-Killed Seeds

VOLUME 41 APRIL, 1950 NUMBER 4

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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The JOURNAL OF HEREDITY is published monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore 11, Md., and 1507 M St., N. W., Washington 5, D. C. Address all communications regarding editorial matters to 1507 M. St., N. W., Washington, D. C. Communications regarding the business management of THE JOURNAL OF HEREDITY may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to 1507 M St., N. W., Washington 5, D. C. Entered as second-class matter February 24, 1923, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917 authorized December 29, 1918. Contents copyrighted 1949 by the American Genetic Association. Unauthorized reproduction of material from THE JOURNAL not permitted. The title "Journal of Heredity" is registered as a trade-mark in the U. S. Patent Office. $5.00 a Year. 50c a Copy. Prices of back numbers on application.

The

Journal of Heredity

Vol. XLI APRIL, 1950 No. 4

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MODIFIED AND NORMAL SQUASH BLOSSOMS

Figure 1

A—Three types of blossoms, normal female (bottom), modified female (top), and normal male (center), produced on the same plant. *B*—Enlarged views of the three types of blossoms. The normal female blossom on the left develops into an elongated fruit while the modified female type (two in center) develops into a spherical fruit. The blossoms shown in each of these photographs came from a single plant.

DIMORPHIC FEMALE BLOSSOM AND FRUIT TYPES

On the Same Plant in *Cucurbita pepo*

LAWRENCE C. CURTIS AND JOHN SCARCHUK*

AT the Connecticut Agricultural Experiment Station, New Haven, Connecticut, in 1945, a most unusual plant was observed in a segregating line of *Cucurbita pepo*. Although the plant—a vining type—was normal in all characteristics, it bore fruits of distinctly different shape. One type was spherical in shape and had a rather long peduncle, while at an adjacent node on the same stem an elongated type with a short peduncle was borne. Figure 2*A* shows two stems of the original plant, one of which has two spherical fruits flanking an elongated type. The second stem has one elongated fruit with two spherical fruits distally located on it.

In 1946 remnant seed of the segregating line was planted at the University of Connecticut at Storrs and during the growing season each plant was carefully observed for the appearance of any similar segregants of the 1945 season.

During the blossoming period, three plants in a row of thirty produced two distinct types of female blossoms as well as male blossoms all of which were normal in every respect. Figures 1*A* and *B* shows the gross external characteristics or these blossoms. The normal female blossom has a short peduncle and the ovary is elongated. The modified female blossom is spherical and the ovary has a long peduncle. The normal female blossoms developed into elongated fruit, and the modified female blossoms developed into spherical fruit.

Attempts to get selfed fruit from both normal and modified female blossoms were successful.

In 1947, seeds from these selfed fruits were planted and each produced plants bearing the two types of female blossoms which in turn developed into either elongated or spherical fruit.

Selfed fruit from the 1947 plants produced plants in 1948 with both types of female blossoms as well as normal male blossoms.

There seemed to be no pattern of production of these dimorphic female blossoms along the stems. Figure 3*A* shows a cluster of five modified female blossoms at four consecutive nodes. Figure 3*B* shows two spherical fruits on either side of an elongated type. In general there were more modified female than normal female blossoms on any given plant.

In so far as we were able to determine there was no association between the occurrence of these dimorphic female blossoms and weather or soil type. The fact that they were observed in only one line, that they appeared in four consecutive years, and that both types of fruit bore seeds which in turn developed into plants the following year which produced both types of blossoms and fruit has led us to conclude that the production of these blossoms and fruit is caused by genetic rather than environmental factors.

What is the Explanation?

In the absence of a definite genetic and physiological analysis of this unusual phenomenon, the writer can only speculate as to the mechanism involved in the production of two such diverse blossom and fruit types on a single stem.

Because the occurrence of both male and female blossoms on a single squash vine is accepted as natural, the hypothesis has been proposed that a chemical

*National Cottonseed Products Assn., Dallas, Texas and University of Connecticut, Storrs, Connecticut, respectively.

MODIFIED AND NORMAL FRUITS

Figure 2

A—Dimorphic fruit types on two different stems of the same plant. Two modified (round) fruits and one normal fruit are shown on each stem—the order of their attachment being different. *B*—Shows the distribution of blossom types on two stems of the same plant. Modified female blossoms or fruits are numbered 1, 4, 5, 6, 7, 9, and 12. Normal female blossoms or fruits are numbered 2, 3, 8, and 11. Numbers 10 and 13 are male flowers. Blossoms 11, 12, and 13 are from another part of the same plant.

NO CONSISTENT ARRANGEMENT

Figure 3

A—There is no consistent pattern in the production of the normal and modified female blossoms along the stem. *A* shows five modified female blossoms on four consecutive nodes on a single stem. A normal female bud is shown at right center, on a secondary stem of the same plant. *B*—Two spherical fruits developed from modified female blossoms on either side of an elongated fruit which developed from a normal female blossom.

substance, or substances, produced by the plant is mobilized at different nodes on a vine and is responsible for the differentiation of a male or female blossom. Sufficiently refined techniques have not been perfected, however, to prove or disprove such a hypothesis.

If such a mechanism is involved in the normal differentiation and production of male and female blossoms in monoecious plants such as the cucurbits, it seems logical to assume that perhaps in this particular line of squash there are three different chemical substances which are mobilized singly or in varying proportions at different nodes to cause the differentiation and development of one of the three different blossom types.

The persistent appearance of this second type of female blossom intrigues the imagination and invites speculation not only as to the cause but also as to how proof of the presence of a chemical sex differentiating substance can be demonstrated. Perhaps if elaborated chemical substances are the causal agents, their presence could be demonstrated by some type of a graft between mono and dimorphic fruit lines.

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GENETICS DIES IN CHINA

A FIRST-HAND account has been received of an eye-witness to the end of "Mendel-Morganist" genetics in China which quickly followed the success of the Communist armies. Prior to the Communist victory, Dr. C. C. Li, author of a notable recent textbook on mathematical genetics, was a member of the faculty of the National Peking University of Agriculture. Writing to a friend in this country Dr. Li details the steps of what has become a tragic routing in all Communist countries:

"Following the entrance of the Communist army into Peking in January, 1949, the same type of controversy (as that in Moscow in 1948) developed in China, particularly in National Peking University College of Agriculture to which I have been attached. In order to present to Chinese biologists and students Lysenko's interpretation of genetics, I, in collaboration with one of my colleagues, translated into Chinese the English translation of Lysenko's "Heredity and Its Variability" last summer. This was published by the Communist party's New China Book Company (Peking, 1950) in January. The first ten thousand copies were sold out in the following two weeks and a second printing of the book is now on the press.

"As you may well visualize, Mendelian geneticists in China have been in an extremely difficult position since Spring, 1949. The situation reached a head when the College was completely taken over by the Communists in the fall. The courses on Mendelian genetics were suspended immeditaely and the spring semester sees the discontinuation of statistics, a course which I offered, on the ground that statistics is at the service of Mendelism! A controversy which had its beginnings in a purely scientific subject has now descended to one of personal abuses. Even with unlimited patience, my colleagues and I have been unable to save the science of genetics from its death in China. The situation becomes one in which one must declare his allegiance to the Lysenko theory or leave. The latter has been my choice.

"I arrived in Hongkong for a rest at the beginning of the month and am planning to make a visit to the United States in the near future. I hope that we shall have the opportunity to meet. If I may be of any service to any of the American universities or institutions that you know of, I should be only too glad to offer them."

Very sincerely yours,
C. C. Li

Invitations to Dr. Li may be forwarded through the office of the A.G.A.
—Ed.

TWIN AND TRIPLET PEPPER SEEDLINGS

A Study of Polyembryony in *Capsicum frutescens*

D. T. Morgan, Jr. and R. D. Rappleye

NUMEROUS instances of plural embryo formation are recorded in the literature for many species of the angiosperms. In most plants where the sexual process is regular as reflected by the consistent production of sexual monoembryonic seeds, polyembryonic seedlings are of limited and sporadic occurrence. However, a relatively high percentage of the seedlings of a few species, primarily polyploid and apomictic, have been established as polyembryonic in origin. Since 1933, when haploid plants were found in twin seedlings of *Linum*[9] and *Oryza*[12], polyembryonic seedlings have been recognized as a source of variants in chromosome number. Subsequently, various combinations of haploid, diploid, polyploid and aneuploid plural seedlings have been reported in a number of species. Since multiple embryo formation is ordinarily an infrequent event, such reports are often based on a relatively small number of polyembryonic individuals. It is the purpose of this study to determine the different polyembryonic types and their frequencies in a relatively large population of a sexual diploid, *Capsicum frutescens*.

Materials and Methods

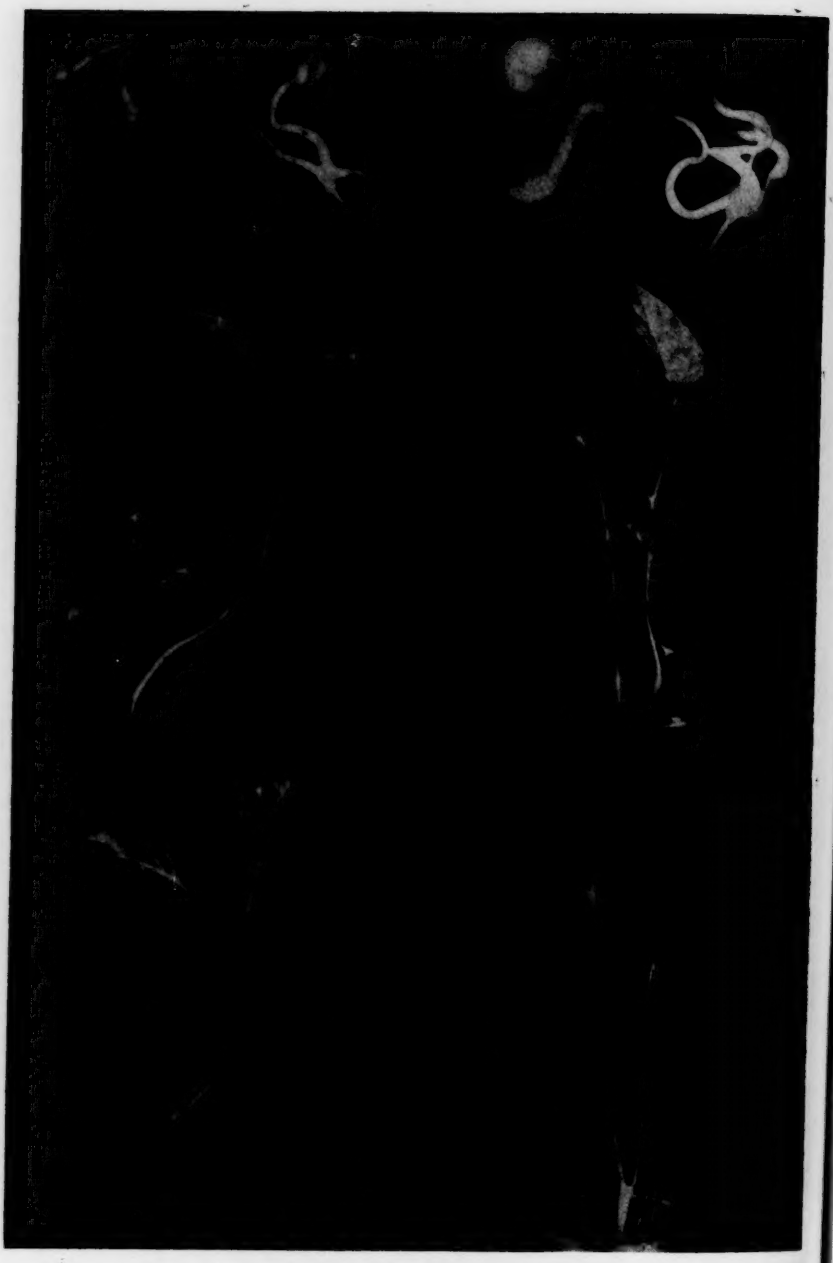
The seeds employed in this study were obtained from plants grown under relatively uniform environmental conditions in large commercial fields. Occasional seeds with fused or partially fused testas were observed in the large groups of seeds collected for analysis. Such seeds, obviously derived from separate ovules, were discarded. The remaining seeds were evenly spaced in groups of 100 on moist paper toweling by means of a vacuum operated seed counting plate. Seedling counts were made at intervals of seven and twelve days after placing the seeds in germinating chambers maintained at 30 degrees centigrade during the day and 20 degrees centigrade at night. Polyembryonic seedlings were selected, transplanted and grown to maturity. The chromosome number for each plant was determined from two separate root tips fixed in Navaschins', embedded, sectioned and subsequently stained by the crystal violet technique.

Results

The data relative to the frequency of polyembryony are summarized in Table I. A total of 294 polyembryonic seedlings was obtained from a population of 78,005 germinated seeds. Of the 294 seeds containing multiple embryos, 291 produced twin seedlings and 3 produced triplets. Statistically significant differences in the frequencies of polyembryony were observed for three varieties tested. The variety Pimento had the lowest frequency of polyembryony and Goliath the highest. An intermediate frequency was observed for the variety California Wonder. Varieties other than Goliath, California Wonder and Pimento are recorded as miscellaneous varieties in Table I due to the comparatively small samples tested for each individual variety.

The different polyembryonic types and their frequencies of occurrence are recorded in Table II. Chromosome counts were obtained for both members of 139 twin pairs and for all the seedlings resulting from the three triplets. Frequently one member of a twin was less vigorous than the other member and failed to survive. In such cases the chromosome number of the viable member is recorded in Table II under the heading "Survivor." Due to temporarily unfavorable growing conditions, many of the twin seedlings of the variety California Wonder did not survive. However, it was possible to grow to maturity all members of 96 of the 157 polyembryonic seedlings obtained from the variety Goliath. As shown in Table II, haploid-haploid, haploid-diploid, diploid-diploid and diploid-tetraploid twins were observed. The diploid-tetraploid and haploid-haploid twins occurred infrequently in comparison with the other types. Conjoined or partially fused diploid-diploid twins were observed but less frequently than diploid-diploid twins of the unattached type. No conjoined twins occurred in which the two plants had different chromosome numbers. All of the members of the triplets were diploid. Several of the polyembryonic types are illustrated in

*Paper No. A-263, Contribution No. 2202 of the Maryland Agricultural Experiment Station (Department of Botany). The advice and encouragement of Dean Ronald Bamford are gratefully acknowledged.



TWIN AND TRIPLET SEEDLINGS

Figure 4

A-D show polyembryonic seedlings as they were removed from the germinating chamber. *E-H* show such seedlings at a later phase of growth. The nature of the twins and triplets shown is as follows: *A*—Haploid-diploid twin seedling. The smaller embryo was haploid. *B*—Unattached diploid-diploid twin. *C*—Conjoined diploid-diploid twin. *D*—Diploid-diploid-diploid triplet. *E*—Haploid-diploid twin: the smaller plant was haploid. *F*—Unattached diploid-diploid twin. *G*—Conjoined diploid-diploid twin. *H*—Diploid-diploid-diploid triplet with the two large members conjoined.

Figure 4. No aneuploids were observed and all of the diploid plants were highly fertile as shown by extensive seed formation. Of the 354 mature plants originating from polyembryonic seeds, 48 (13.6 percent) were haploids. The haploid plants were characterized phenotypically by their sterility, small size and elongate leaves. A haploid chromosome complement of 12 was observed confirming the reports of previous investigators.[3,8,16]

Discussion

The extensive literature in reference to polyembryony has been summarized previously by Webber.[17] Christensen and Bamford[3] who found haploid plants in a population of twin seedlings of *C. frutescens*, have discussed most of the pertinent literature in regard to the present study. Consequently, a survey of the literature will not be attempted in this paper.

The data of Table I show varietal differences in the frequencies of polyembryony. Plural seedlings are approximately ten times as frequent in the variety Goliath as in the variety Pimento. Varying frequencies of polyembryony may be attributed to differences in environmental conditions and varietal genotypes. However, since the seeds employed in this study were collected from plants grown under relatively uniform environmental conditions, it seems likely that differences in polyembryonic frequency of the magnitude reported in Table I could not be due primarily to varying environmental factors. Moreover, since *C. frutescens* is characteristically a self-pollinating species with numerous clearly differentiated varieties, it would appear that the several frequencies of polyembryony reflect differences in varietal genotypes. Previous investigators have found intraspecific differences in frequencies of polyembryony for several species.[10,14,17] In *Linum*, Kappert[9] obtained lines with high frequencies of polyembryony by selection from the progeny of crosses between strains with low frequencies. Recently, varying frequencies of polyembrony have been reported for different genetic strains of *Nicotiana tabacum*[2] and *Asparagus officinalis*.[13] Perhaps the most convincing evidence for the effect of the genotype on polyembryonic frequency in *C. frutescens* will develop from the analysis of crosses between highly homozygous lines exhibiting extreme differences in frequencies of polyembrony. Homozygous diploids have been produced by colchicine treatment of the haploids obtained in this study for use in the further analysis of the effect of the genotype on polyembryony.

In the absence of specific morphological or genetic information any classification of the polyembryonic types in regard to origin must necessarily be speculative. Webber[17] states that polyembryony may often be a complex and variable process. However, it seems likely that the conjoined diploid-diploid twins arose from an embryonic split during ontogeny and would be classified under

TABLE I. Varietal frequencies of polyembryony

Variety	Dormant seeds	Germinated seeds	Monoembryonic seeds	Polyembryonic seeds: Twins	Polyembryonic seeds: Triplets	% Polyembryony
California Wonder	45,574	39,562	39,450	112	0	0.28
Goliath	31,654	24,182	24,025	154	3	0.65
Pimento	7,800	6,608	6,604	4	0	0.06
Misc. varieties	14,583	7,653	7,632	21	0	0.27
Total, all varieties	99,611	78,005	77,711	291	3	0.38

TABLE II. Frequencies of polyembryonic types

Variety	Twins: N-N	N-2N	2N-2N (1)	2N-2N (2)	2N-4N	Triplets: 2N-2N-2N (3)	2N-2N-2N (1)	Survivors: N	2N
California Wonder	1	7	24	3	0	0	0	1	28
Goliath	1	32	44	15	1	2	1	2	25
Pimento	0	2	2	0	0	0	0	0	0
Misc. Varieties	0	0	6	1	0	0	0	0	11
Total, all varieties	2	41	76	19	1	2	1	3	64

(1) Unattached.
(2) Conjoined
(3) Two members conjoined; one separate

Webber's category of cleavage polyembryony. Fusion or natural grafting between two separate diploid embryos offers an alternative explanation for the origin of the conjoined types. However, since both members of the conjoined pairs were invariably diploid, it would appear that embryonic fusion, if it occurred at all, was necessarily restricted to embryos of the same chromosomal constitution. The unattached triplet and diploid-diploid twins may represent examples of cleavage polyembryony at an earlier developmental stage than the conjoined twins or may conceivably be derived from different combinations of apomictic and sexual embryos originating from one or more embryo sacs. Preliminary results from further research on the origin of the polyembryonic types indicate that the majority of the diploid-diploid twins are sexual in origin. Cooper[5] in several species of *Lilium* observed the embryological development of haploid-diploid twins and concluded that the haploid embryo arose from a synergid stimulated to divide following fertilization. Androgenetic haploids, usually following interspecific and intergeneric pollinations, and haploids arising from somatic reduction in integumental cells of an apomictic species have also been reported.[4,6] However, since *C. frutescens* is ordinarily a self-pollinating sexual diploid, it seems likely that the haploid plants in the twin seedlings arose from reduced cells of the female gametophyte.

Various investigators have commented on the use of haploids in plant breeding studies.[1,3,7,11,13,14,15] Toole and Bamford[15] obtained homozygous diploids by colchicine treatment of *C. frutescens* haploids. Similarly colchicine treatment has doubled the chromosome complements of thirty of the haploids obtained during the present study. Since haploid plants may be readily obtained and their chromosome complement conveniently doubled, a technique for their utilization in the development of new varieties became apparent during the present study. Haploids originating from the gametophytes of the F_1 following intervarietal crosses could be obtained and subsequently treated with colchicine. The resultant doubled haploids would have different combinations of characters due to meiotic segregation in the F_1 hybrid. In a self-pollinated diploid species like *C. frutescens*, selection of desired types from the different doubled haploids would immediately result in the isolation of new homozygous varieties. If one parental variety possessed the majority of favorable characters, one or more generations of backcrossing to the superior variety prior to the isolation of the haploids would presumably greatly increase the chance of obtaining the desired type of double haploid.

Summary

1. Varieties of *C. frutescens* having high, low and intermediate frequencies of polyembryony were observed. The several frequencies are believed to reflect intrinsic differences in varietal genotypes.

2. Three triplet and 291 twin seedlings were obtained from 78,005 germinated seeds. Chromosome counts disclosed the following twin types which are listed in ascending order of their frequencies: diploid-tetraploid, haploid-haploid, conjoined diploid-diploid, haploid-diploid, and unattached diploid-diploid. All members of the triplet seedlings were diploid. Possible modes of origin of several of the polyembryonic types are discussed.

3. Thirty of the haploid plants from the polyembryonic seedlings have been treated with colchicine to produce homozygous diploids. The doubled haploids thus obtained are being employed in genetic and plant breeding studies.

4. A method is discussed for the utilization of haploids in developing new homozygous varieties.

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THE CHROMOSOMES OF VERTEBRATES

A REVIEW

THE author's purpose in writing this book* is clearly stated in the introduction. It is to assemble and critically examine the information which has accumulated on the cytology of vertebrates. This project was an ambitious one, but one long overdue. The result is a book which is all that can be desired in a work of this kind. Professor Matthey has not only brought his subject up to date, he has also been most successful in "sifting the grain from the chaff."

The book is free of gross errors and the omissions are deliberate. The Latin names of animals are quoted without authorities and plates lack dimensional scales. These have both been omitted to avoid possible error, since so many workers fail to be specific on these points. In any case, references are always given and workers may, if they wish, refer to the original works and form their own conclusions.

Four chapters, an appendix of thirty-five plates, a complete bibliography and a zoological index make up the book.

Chapter I is titled "Technique." The various methods of fixation are appraised and the value of the more important summarized in tabular form. Only two paragraphs are used to discuss stains; these however, constitute a good resume of the subject which is probably all it warrants in a book of this type. The remainder of the chapter is devoted to methods of examination, pointing out the difficulties and pitfalls to be avoided in the examination and interpretation of the preparations. The chapter, while brief (34 pages) should prove an invaluable guide to beginners as well as established workers.

The second chapter "Historical" is a critical review of the general contributions and conclusions of most of the vertebrate cytologists from the time of Schottländer (1888) to the present time. The available general information on the chromosome make-up of the five vertebrate classes is well covered. Sweeping generalizations are not only avoided but those made by some workers are pointed out and numerous errors and misinterpretations corrected.

Chapter III is devoted to "Sex Chromosomes." The subject is given the most careful and critical treatment. Whenever necessary, the author does not hesitate to interpret cytological data in the light of information supplied by genetics. However, the approach remains primarily a cytological one. The cytological basis of sexuality in mammals is covered by a summary of the contributions of Winiwater, Painter, Minouchi, Oguma, Makino, Koller and Matthey; then by reviewing the work of a number of authors on various mammals including man. The danger of all-inclusive generalizations is again brought out and illustrated by the work of Matthey and his pupil R. Bovery with *Sorex araneus.*

The final chapter "Chromosome Evolution, Phylogeny and Systematic Relationships" deals first with observed and hypothetical mechanisms of chromosome evolution, drawing freely from the more abundantly available information provided by insect and plant cytology. Finally, an extensive treatment is given to the problem of the evolution of chromosome systems in vertebrates, based on comparative studies made within and between the various classes.

The body of the text is illustrated with nicely drawn figures. The appendix consisting of thirty-five plates grouping 442 figures shows the same painstaking workmanship and careful detail.

In *Les Chromosomes Des Vertebres* Professor Matthey has succeeded in preparing not only an atlas of vertebrate chromosomes, he has also brought together most of the pertinent information on the subject as well as its many theoretical considerations. Besides being a valuable source of information for workers in vertebrate cytology, it should also be of more than passing interest to those interested in genetics, evolution and the other allied subjects.

L. A. DIONNE
University of Wisconsin

*MATTHEY, ROBERT, *Les Chromosomes Des Vertebres.* Librairie de l'universite, F. Rouge Lausanne. 1949.

GENETICS JUBILEE—SEPTEMBER 11-14, 1950

THE Genetics Society of America at its annual meeting on December 29, 1949, voted to celebrate in 1950 the 50th birthday of the rediscovery of Mendel's fundamental work. Furthermore, genetics as a science began with the rediscovery of Mendel's original findings, so this proposed celebration may justifiably be called the Golden Jubilee Program of Genetics.

The meetings in 1950 of the Genetics Society are to be held at Columbus, Ohio from September 11 to 14, under the auspices of the American Institute of Biological Sciences. The first day of the meetings of the Society will be given over to the presentation of short papers describing the results of current research.

A general meeting of all the biological societies which will convene at Columbus is scheduled for the evening of Monday, September 11, at which the keynote address on "The Impact of Genetics on the Biological Sciences," will be given by R. B. Goldschmidt, Emeritus Professor of Zoology at the University of California. This address will mark the beginning of the Golden Jubilee Program.

The papers to be given on Tuesday, September 12, will include various considerations of "Historical Aspects and the Development of Genetics." On Wednesday morning, September 13, the general topic is "The Physical Basis of the Gene," and that of the afternoon is "The Physiology of the Gene." Three papers on "Cytogenetics" are scheduled for Thursday morning, September 14, to be followed by several dealing with "Genetics and the Food Supply" and "Genetics, Medicine and Man."

The addresses of the President of the American Society of Naturalists and of the President of the American Society of Human Genetics are to be a part of the Golden Jubilee Program.

The final address will be delivered on the evening of Thursday, September 14 by Julian Huxley, until recently Secretary-General of UNESCO, under the title of "Genetics, Evolution and General Thought."

The speakers at the Golden Jubilee Program will survey the development and present status of various phases of genetics. In addition, each speaker is invited to consider probable paths of future thought and discovery. The papers are to be published as a separate volume. In addition to the sales which are anticipated in the United States and Canada, arrangements are being made for a wide distribution of the publication abroad.

Mammary Tumors in Mice

THE purpose of this Symposium* by Members of the Staff of the National Cancer Institute is two-fold. "The first is to present to the cancer research worker and to readers more casually interested in this field up-to-date and coordinated knowledge of cancer of the breast in mice. Secondly, and what is perhaps more important, it cannot fail to stimulate interest and further research efforts in one of our most fascinating and important biologic problems."

The ten contributors, representing various biological specialties, have recognized the value of a concentration upon one particular type of cancer in one particular species and state: ". . . such an approach is of value because, it emphasises the danger of reasoning from one type of malignant disease in one species to possible divergent types of cancer in other species, and because it reveals the magnitude and the complexity of the cancer problem as a whole."

Readers of the Journal will be especially interested in the Genetics of Mammary Tumors in Mice by Dr. Heston. At present three paths through which differences in genic action affect the probability that a mammary tumor will appear have been identified. There is evidence that genic differences can influence (1) the response of the mammary tissue cell to the hormonal stimulation and to the milk agent stimulation, (2) the occurrence of mammary tumors through the hormonal mechanism, possibly in controlling the production of hormonal stimulation, and (3) the propagation and transmission of the milk agent. Since it has not been demonstrated that the milk agent is limited to any particular tissue, one cannot predict just where the genic action occurs in the last case. Mammary tumors do not result from any one of these genic factors or sets of factors, but from the action and interaction of all.

The biologist will find many items of interest in this thorough report, *i.e.* information about diet, hormones, the virus-like milk agent, and about cancer itself.

Although the book was published in 1945 it is still important and certainly the most complete dealing with mouse mammary tumors.

GEORGE W. WOOLLEY

Sloan-Kettering Institute

*Moulton, Ray Forest, Editor. A Symposium on Mammary Tumors in Mice by Members of the Staff of the National Cancer Institute. Publication of the American Association for the Advancement of Science No. 22. Lancaster: Science Press 1945. 223 pages.

RESUSCITATION OF HEAT-INACTIVATED SEEDS BY X-RADIATION*

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THE interesting findings of Caldecott and Smith[1] reported in this JOURNAL, in which "seeds exposed to lethal heat treatment could be resuscitated by subsequent exposure to X radiation" appeared to offer possibilities for additional study. Consequently, similar investigations were conducted to determine the effects of post-irradiation on seeds, following sublethal and lethal heat treatment. It was found that the striking observations of Caldecott and Smith, involving a heat-inactivation/X-ray-reactivation phenomenon could not be duplicated at this laboratory.

Methods of Treatment

In conducting the experiments, care was taken to follow the procedure of Caldecott and Smith, although variations obtained here required some revision of the original method. The seeds were of the same genetic stock of Himalaya barley and einkorn‡ used by Caldecott and Smith, and kindly furnished by Dr. Smith.

In determining the lethal temperature of barley and wheat seeds, Caldecott and Smith used an electric oven. In attempting to work with an electric oven at this laboratory, it was found that in five-minute or shorter periods the oven temperature varied as much as ±15° C. from the desired point of treatment. Consequently, a modification of the original method of heat treatment was necessary. It was suggested§ that an Abderhalden drying apparatus could be adapted for heat treatment. A diagram of the apparatus is presented in Figure 5.

In using this method of heat treatment, care was taken to select liquids of constant boiling point in order that the temperature could be maintained to within ± 0.5° C. of the desired treatment point for the 30-minute exposure period. The size and shape of the brass seed receptacle was designed to bring about maximum heat retention within the glass treatment tube, and the problem of temperature change in the tube following insertion and withdrawal of seeds was eliminated for all practical purposes. The seeds were placed in a single layer in two narrow slots inside the brass cylinder, and so were enclosed by the brass. The temperature was measured through a thermometer adapter hole in each half of the brass cylinder, and the readings were identical. All heat treatments were carried out in the Abderhalden apparatus.

The X-ray unit was operated at 250 Kv. peak and 15 milliamperes, with 3 mm. aluminum inherent filtration, giving an intensity of 1350 r/min. at the surface of the seeds. The seeds were placed on a lucite tray in a field having a diameter of approximately 1½ inches, assuring uniform intensity at the surface of all seeds. Each X-ray treatment was preceded by Victoreen meter monitoring. The seeds were subjected to a total dose of 12,000 r of X-rays. This dose was selected since it was the one producing the greatest observable "resuscitation" of heat-inactivated seeds in the experiments conducted by Caldecott and Smith, yet produced no killing when used alone. In one experiment an X-ray dose of 24,000 r was used to check the effect of increased dosage on seed survival.

Seeds were planted in vermiculite in seed boxes, and placed in the greenhouse. Survival was recorded daily by a count of the number of germinated seeds (seeds which broke the surface of the vermiculite) until maximum germination was attained which, in some cases, took as long as ten days. Results were expressed in percent survival.

The experimental procedure was as follows:

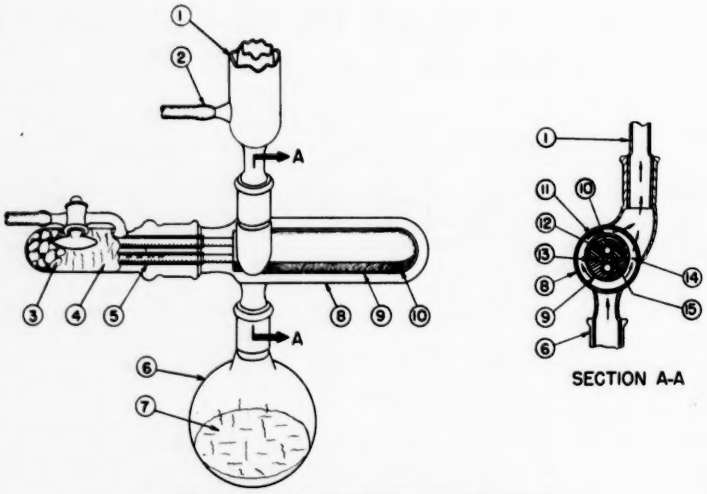
1. Fifty seeds were heated at the desired temperature for thirty minutes. Twenty-five of these seeds received no further treatment, and were designated as the "heat-alone" group.
2. The other twenty-five heat-treated seeds were given 12,000 r of X-rays closely following the heat treatment. This was the "heat + X-ray" group.

*Work performed under Contract No. W-7405-eng-26 for the Atomic Energy Commission at Oak Ridge National Laboratory, Oak Ridge, Tennessee.

†The author wishes to express his appreciation to Dr. Alan D. Conger of this laboratory for his helpful suggestions in some of the experiments.

‡The einkorn wheat was used to determine the initial heat-survival curve. Only barley seeds were used in the humidity and heat + X-ray experiments.

§The idea of adapting the Abderhalden drying apparatus for heat treatment was suggested by Dr. Martin Kuna, formerly of this laboratory, and Dr. David G. Doherty of this laboratory.



ABDERHALDEN HEATING APPARATUS

Figure 5

The elements of this devise are as follows:

1. Distilling Tube;
2. Water Inlet;
3. Anhydrous Calcium Chloride;
4. Cotton;
5. Thermometer;
6. Round Bottom Flask;
7. Constant Boiling Liquid;
8. Outer Jacket;
9. Inner Treatment Tube;
10. Brass Holder;
11. Constant Temperature Vapor Circulation;
12. Thermometer Hole;
13. Seed;
14. Air Space; 15. Seed Groove.

Thermometer hole (Item 12) and seed groove (Item 15) extend the entire length of brass holder (Item 10).

3. Twenty-five untreated seeds were X-rayed simultaneously with the "heat + X-ray" seeds, and these were called the "X-ray-alone" group.
4. Twenty-five seeds received no treatment at all and served as the control group.

It should be stressed that in each individual treatment at a specific temperature, the fifty seeds initially heated for thirty minutes were subdivided following heating, and twenty-five of these seeds then X-rayed. Hence there was no possibility of a difference in heat treatment, as both groups, the heat alone and the heat + X-ray, received the same heat treatment at the same time.

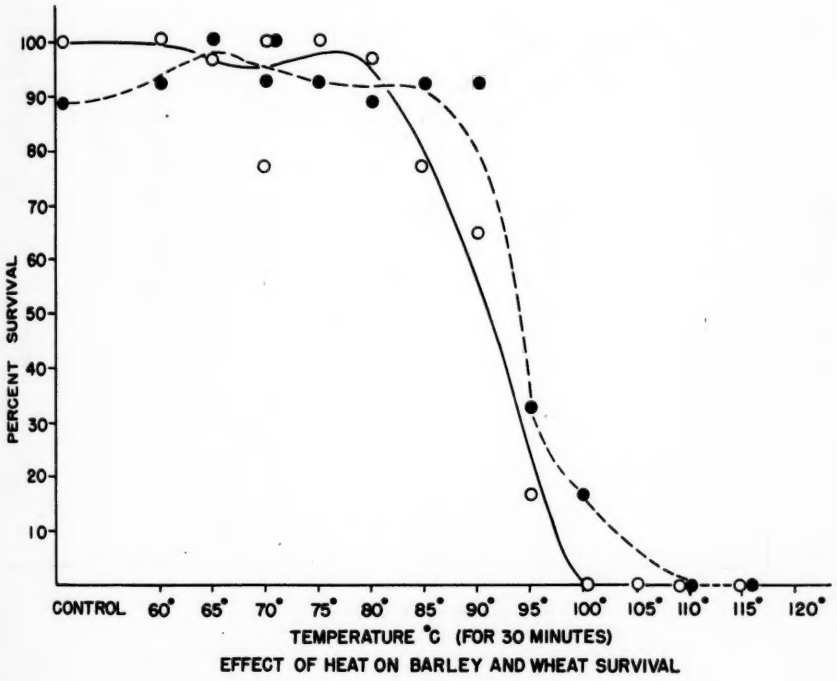
As the work progressed, it was found that the 100 percent-lethal temperature of the seeds had shifted appreciably from that value obtained in the original heat survival curve. Consequently, several experiments were conducted with desiccated and undesiccated open-stored seeds to estimate the effect of variable humidity on their lethal temperature. Half the seeds were placed in a desiccating jar containing anhydrous calcium chloride, where they remained for a minimum of three days prior to removal and subsequent heat/X-ray treatment. Although no quantitative estimate of the reduced moisture content of the desiccated seeds was made, it is reasonable to assume that it was appreciably less than that of the non-desiccated seeds. The experimental procedure as given previously was unchanged, and for each step the desiccated and undesiccated seeds were treated simultaneously.

Results

It was first necessary to establish a lethal temperature (zero survival), and for this, both barley and wheat seeds in twenty-five-seed lots, were treated for thirty minutes. A range of temperatures from 60-115° C. was covered at about 5° C. intervals. The data are given in Table I and presented graphically in Figure 6.

It was observed that zero survival was first obtained at a temperature of 100° C. for barley seeds, and 110° C. for wheat seeds. In both cases the survival curve tapered off gradually from greater than 90 percent survival to zero survival within a range of approximately 20° C. It was found that the lethal point was subject to change, and shifts of as much as 11° C. were observed in the three months during which this work was done. These data are given in Table II and presented graphically in Figure 7.

In the experiments conducted to determine the possible effect of humidity on the lethal



TEMPERATURE SURVIVAL CURVE

Figure 6

The open circles and solid line (○——) show barley; the solid circles and broken line (●----) show wheat. With no control of moisture content of the treated seeds, the curves are not markedly different.

temperature of barley seeds, those seeds which had been desiccated prior to heat treatment showed a much greater resistance to heat than did the seeds which had been left in an open jar. (Table II and Figure 7.)

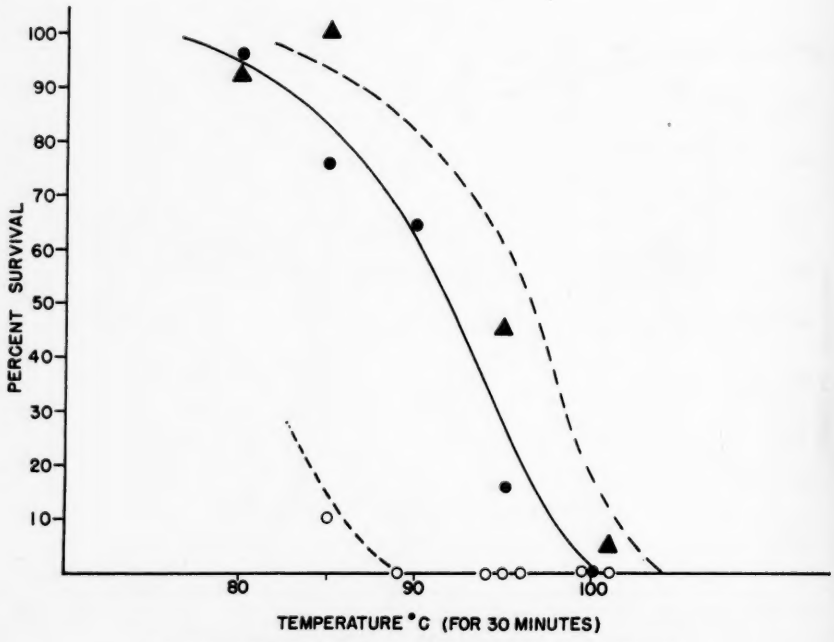
In no case did the present experiments indicate the existence of the striking "resuscitation" of heat-killed seeds with X-rays reported by Caldecott and Smith. Finally, assuming that there may be some possible difference in X-ray response between seeds which have been killed by barely lethal heat treatment (resulting in about 10 percent survival), and those which have been killed by a thoroughly lethal treatment (resulting in zero survival), barley seeds were heated at temperatures permitting low survival. This was followed by X-radiation, and in no case was any "resuscitation" found to exist in the heat + X-ray group.

It should be reported however, that two apparently real, though anomalous, results were obtained with the desiccated seeds. In one case, after heat treatment at 92° C., X-rays seemed to exert a depressive effect on seed survival. Later, following heat treatment at the same temperature as above, a single in-

TABLE I. Survival of dormant seeds of barley and einkorn wheat following heat treatment for 30 minutes at temperatures indicated. Each treatment consisted of 25 seeds, and all treatments were given on April 29.

Temperature ° C. (For 30 minutes)		Control	60°	65°	70°		75°	80°	85°	90°	95°	100°	105°	110°	115°
Barley	Percent Survival	100	100	96	76 100	88*	100	96	76	64	16	0	0	0	0
Einkorn Wheat		89	92	100	92 100	96*	92	88	92	92	32	16	4	0	0

*Average of two 25-seed lots. Treated on two successive days.



EFFECT OF DESSICATION ON BARLEY SURVIVAL

Figure 7

The improved survival of seeds which were dried before heat treatments is shown here. The solid circles and the solid line (●——) show result of heat treatment of undesiccated seeds on April 29, 1949. The open circles and open line (○- - - -) show the results of tests made between May 31 and August 1, 1949. The triangles and broken line (▲- - - -) show the survival curve of desiccated seeds tested between May 31 and August 1, 1949.

stance of apparent partial "resuscitation" was observed. These were the only two experiments out of the seventeen treatments carried out which demonstrated a significant difference of any sort between the heat-alone and the heat + X-ray groups. This is presented in Table III and Figure 8—experimental points at 92° C.

The seeds which received only X-radiation and those which received no treatment exhibited above 96 percent survival in all cases. In the single instance using 24,000 r of X-rays, no apparent effect of the increased dosage on seed survival was noted.

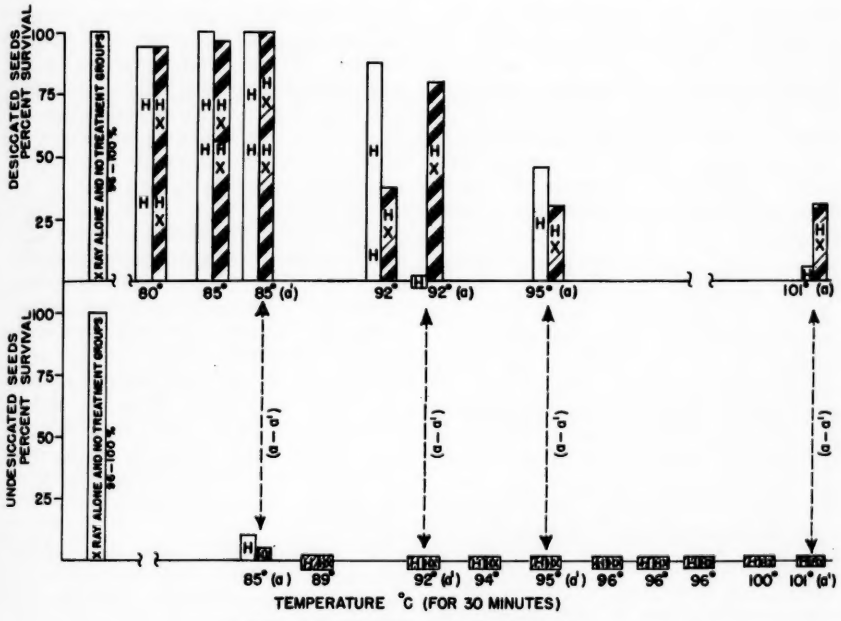
Discussion

Although this experiment was conducted on a pattern following that of Caldecott and Smith, there were several fundamental differences which might ac-

TABLE II. Comparison of lethal temperatures of barley seeds following 30-minute heat treatment. Shift is demonstrated over the three-month period from April 29 to August 1. Results are expressed in percent survival at the temperatures indicated.

Groups	Temperature in ° C (for 30 minutes)									
	Controls	80°	85°	89°	90°	94°	95°	96°	100°	101°
Undesiccated barley seeds. Treated April 29.	100	96	76	—	64	—	16	—	0	—
Undesiccated barley seeds. Treated May 31-Aug. 1.	96-100	—	10*	0	—	0	0*	0	0	0
Desiccated barley seeds. Treated May 31-Aug. 1.	96-100	92	100	—	—	—	45*	—	—	5*

*Treatments consisting of 20 seeds. All other treatments—25 seeds.



EFFECT OF HEAT AND X-RAYS

Figure 8

Effect on survival of various dosages of heat and X-rays of barley seeds. Three categories of tests of undesiccated seeds are included: X-ray alone (columns so marked); heat alone (open column marked "H"); Heat plus X-ray (cross-hatched columns marked "H-X"). The only tests which are critical are those of desiccated and undesiccated groups treated simultaneously. These four tests are designated (a—a').

count for the contrasting results. Caldecott and Smith utilized an electric oven for their heat treatment, but it was found at this laboratory that such a method, depending on warm air circulation to replace the cool air layer around the seeds, was accurate only within a 10-15° C. range over a 30-minute period. The

TABLE III. Survival of desiccated and undesiccated dormant seeds of barley given 12,000 r of X-rays following treatment at the indicated temperatures. Only those desiccated and undesiccated groups treated simultaneously can be compared. Results are expressed in percent survival.

				Temperature ° C (for 30 minutes) in Abderhalden apparatus																	
				80°		85°		89°		92°		94°		95°		96°		100°		101°	
Groups	Control	X-Ray Alone		Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray	Heat	Heat + X-Ray
Desiccated (controlled humidity)	96-100% in all 17 experiments	96-100% in all 17 experiments	A	92	92	100	96			88	36			45*	30*					5*	30*
			B			100*	100*			0†	80†										
Undesiccated (uncontrolled humidity—room conditions)			A′					0	0			0	0	0*	0*	0	0	0	0	0*	0*
			B′			10*	5*			0†	0†					0	0				
																0	0‡				

A-A′—Treated simultaneously.
B-B′—Treated simultaneously.

* 20 seeds.
† 15 seeds.
All others, 25-seed treatment.

‡ 24,000 r of X-rays.
All other, 12,000 r X-ray doses.

adaptation of the Abderhalden drying apparatus for heat treatment proved satisfactory, and temperatures could be maintained with much greater accuracy. The use of the brass seed receptacle as a heat conductor rapidly displaced the cool air layer around the seeds, and within a short time the brass and seeds were equilibrated at essentially the same temperature.

The fundamental design of the Abderhalden apparatus prevented the introduction of poisonous vapor into the treatment chamber during the 30-minute heating period. In addition, the work was carried on under a hood, and the water jacket condenser was well cooled, thereby preventing poisonous vapor entry into the treatment chamber during the insertion and removal of the seeds. All treatment apparatus was frequently washed in warm water and Calgonite.

Caldecott and Smith found that following heat treatment, barley and wheat seeds dropped from 100 percent survival to zero survival within a range of 5° C., and in plotting their survival curve the slope was exceedingly steep. They found the lethal temperature of barley to be 70° C. and wheat to be 75° C. The data obtained at this laboratory show a range of approximately 25° C. and 45° C., respectively, for barley and wheat between their 100- and 0 percents survival temperatures. This, when plotted to the same scale, exhibited a more gentle slope. The lethal temperature for barley was initially found to be 100° C. and that of wheat to be 110° C. In the first barley heat-survival curve obtained in April 1949, 100° C. was found to cause 100 percent killing. However, repeated experiments from May 31 to August 1 revealed a significant shift in 100 percent lethality toward a lower temperature. Simultaneous experiments conducted with desiccated seeds (controlled humidity—lower moisture content) and with undesiccated seeds (uncontrolled humidity — higher moisture content) showed that the desiccated seeds required a significantly higher temperature to effect 100 percent killing (Table II and Figure 7). Consequently, if only one heat-survival curve had been plotted initially, and an intercomparison of all subsequent heat/X-ray treatments made with this, it would give entirely misleading results. Rather, it is necessary to make intracomparisons only within each simultaneous heat-alone and heat + X-ray group.

In the work performed here, in each individual experiment a single group of seeds was heat treated, and from this "reservoir," one-half were removed to be further treated with X-rays. Consequently, both the heat-alone and the heat + X-ray seeds were subjected to a common heat treatment. Thus, a reliable comparison could be made regardless of any shift in lethal temperature, so long as intracomparisons only within each simultaneously treated group were involved.

No "resuscitation" was observed on any scale approximating that previously reported. Concerning the single anomalous case of a "resuscitative" and a "depressive" effect of X-rays following heat treatment, there is no satisfactory explanation available. It was not possible to duplicate the results, and until further evidence can be presented, the explanation must be laid to some unknown, uncontrollable variable or variables which, in addition to or in certain combination with heat and X-rays, produced these results. However, this one case was in no way comparable to the consistent 90 percent (or greater) "resuscitation" reported by Caldecott and Smith. In itself it is of little significance.

Summary

1. Experiments have been performed to investigate the reported existence of "resuscitation" of heat-inactivated seeds by X radiation.

2. This previously reported effect was not confirmed.

3. A shift in lethal temperature may be explained by a variation in moisture content in the seeds, increased humidity resulting in lower lethal temperature.

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1. Caldecott, R. S. and L. Smith. *Jour. Hered.* 39:195-198. 1948.
2. Smith, L. and R. S. Caldecott. *Jour. Hered.* 39:173-176. 1948.

A DWARF MUTATION IN A NEMATODE

A Morphological Mutant of *Rhabditis briggsae*, a free-living soil nematode

VICTOR NIGON AND ELLSWORTH C. DOUGHERTY†

THE free-living soil nematodes of the superfamily Rhabditoidea and particularly those belonging to the genus *Rhabditis* Dujardin, [1844] (*sensu lato*), present an assemblage of characters that have led us to the belief that these animals might constitute an exceptionally favorable material for genetic studies.[3,4] A cursory survey shows in fact that their very short reproductive cycle (three to eight days at 20° C), their generally high fertility, and the simplicity of practical culture methods, all justify the hope that one should be able to obtain and study numerous descendants in the course of research on their heredity. Other, more specific characters may be added to the preceding. For example, nematodes fall among that group of Metazoa exhibiting the phenomenon of eutely (*i.e.*, in the so-called "aschelminth" phyla); that is to say, they characteristically have fixed numbers of somatic nuclei in cells and syncytia. It thus seems probable that genetic modifications involving the number and dimension of one or another category of cells should translate themselves in these animals into evident morphological modification. Moreover, the existence in the nematodes of autogamous methods of reproduction (hermaphroditism and parthenogenesis) permits one to predict that the probability of observing the phenotypic expression of a mutation occurring in the germ cells of such forms is much increased over the probability of so doing in the case of a dioecious species. As a matter of fact, whereas in a dioecious species a recessive autosomal mutation occurring in a single germ cell is demonstrable at the earliest in the third filial generation, such can already have manifested itself in the second generation, in a self-fertilizing hermaphroditic species, or even in the F_1 in a wholly or partially parthenogenetic species wherein, as with *Rhabditis belari*, diakinesis initially involves the formation of apparently normal tetrads.[12] Moreover, recent success in obtaining in an axenic medium (*i.e.*, without other living organisms) growth of *Rhabditis briggsae* equal to that in the presence of bacteria suitable as food,[7,8] points the way toward development of a chemically defined medium to permit studies on the biochemical genetics of nematodes.

In connection with the foregoing favorable arguments for the genetic study of *Rhabditis* there must be mentioned, however, the presumably small number of morphological characters capable of varying without impairing the vitality of these animals. Their rudimentary organization might in fact lead one to predict that most mutations involving gross structure (and hence morphologically visible) would exercise a lethal effect. These fears have been in part strengthened by our discovery of a morphologi-

*The present study was largely carried out at the Laboratoire des Travaux Pratiques de Biologie Animale, Faculté des Sciences P.C.B., Université de Paris.

†Laboratoire de Zoologie, Faculté des Sciences, Université de Lyon (senior author); University of California (Berkeley) and Kerckhoff Laboratories of Biology, California Institute of Technology (junior author). While in France, the latter was a fellow of the John Simon Guggenheim Memorial Foundation (1947-1949), and U. S. National Cancer Institute Postdoctorate Fellow (1947-1948). At present Dr. Dougherty is Senior Research Fellow of the American Cancer Society as recommended by the Committee on Growth of the National Research Council (1949-1952). The authors wish to express sincere appreciation to Dr. Spencer W. Brown of the Division of Genetics, University of California (Berkeley), for taking the photomicrographs used herein and to Dr. Curt Stern of the Department of Zoology for critically reading the manuscript.

cal mutant of *R. briggsae* in which vitality has been considerably reduced by contrast with that of the *wild* type. This mutant is the first of morphological type to be demonstrated conclusively in the phylum Nematoda, and the first of any kind of which the inheritance has been worked out. It has been briefly described in a published abstract.[13] Hertwig[10] observed what was apparently a spontaneous mutation from normal dioecious to pseudogamous sexuality in *Rhabditis pellio*, but did not attempt to work out its inheritance, although this might conceivably have been accomplished if she had crossed the rare males occurring in the progeny of the pseudogamously reproducing females with normal females. Graham[9] described morphologically distinct lines of common ancestry in the parasitic rhabditoid, *Strongyloides ratti*, but did not carry out studies to demonstrate what genetic basis these changes had; it seems quite likely that he was dealing with genetic differences, possibly with mutations. No other mutant has been described, to our knowledge in the phylum.

In the work described in the following sections the general experimental techniques used by Nigon[12] have been followed.

Description of the Mutant

The wild type of *R. briggsae*, Dougherty and Nigon, 1949 (Nematoda: Rhabditidae) from which the mutant form originated, has been named and briefly described in a short abstract[6] and described at length in another publication.[14]

It is distinguishable from the very closely related *Rhabditis elegans* Maupas, 1900, by consistent, although minimal morphological characters; furthermore by the fact that the two species have proved intersterile. They are, on the other hand, similar in consisting of hermaphrodites and rare males, of which the latter can be isolated with individual hermaphrodites so that copulation can occur and a progeny with a male proportion sometimes approaching that found in normally dioecious species be produced. Usually, however, the hermaphrodites are self-fertilizing and apparently only produce males as the result of a rare meiotic accident, probably no oftener than about 1 in 500 individuals.

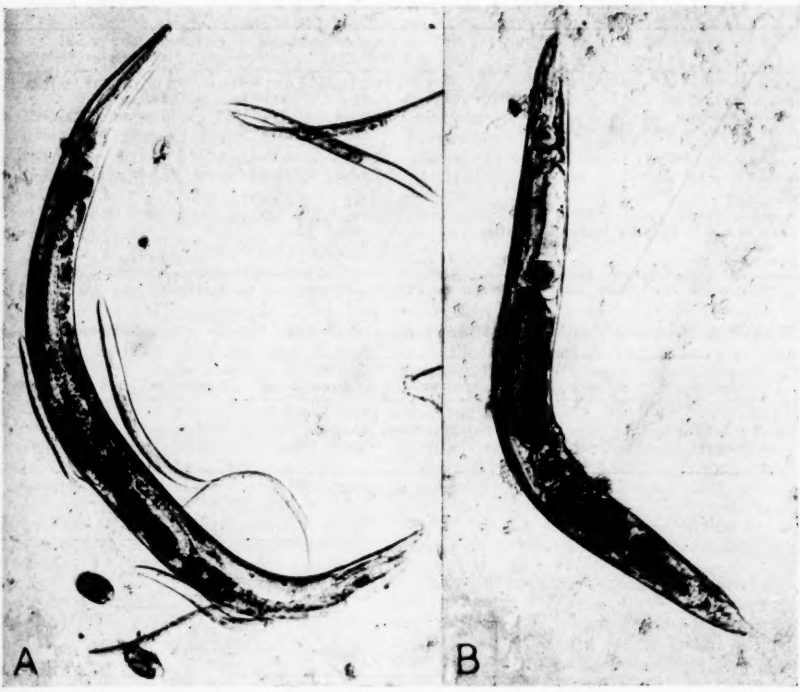
The mutant individuals are to be distinguished from the *wild* type principally by their strikingly reduced size (Figure 9). For this reason we have designated the new form, *micro*. Dimensions for *wild* type and mutant respectively, obtained from animals that had just reached sexual maturity, are given in Table I. Photomicrographs of living *wild* type and *micro* hermaphrodites are given in Figure 9. Figure 10 illustrates the bursae of males of the two forms in lateral view.

Most parts of the mutant appear to be reduced in an identical manner, that is by about a quarter when compared with the *wild* type. We should note, however, that the dimension of the eggs is about the same in both forms. Moreover, the isthmus of the esophagus often has a buckled shape in the mutant animals as if this organ were compressed within a wall too short to contain it. However, this modification is perhaps due to a compression produced by the accumulation of eggs in the uteri.

Despite the difference in length *micro* hermaphrodites are as wide as those of the *wild* type, a fact which gives to the mutant a strikingly thickened appearance. This impression is further accentuated by the relative immobility of the mutant, which is much less agile than are the hermaphrodites of *R. briggsae* habitually. As in the *wild* type the mutant is hermaphroditic, and the descendants of such self-fertilizing hermaphrodites consist of animals resembling their parents. We have only observed 1 male among 930 progeny obtained from individually isolated hermaphroditic parents. However, more recently one of us (Dougherty), having left a *micro* culture in a Petri dish on a laboratory desk for a few days during a warm spell in California (with daytime temperatures up to 25° C), observed numerous males in the resulting population. These could be observed in active copulation with the accompanying hermaphrodites. It is thus probable that *micro* has a response to elevated temperature similar to that of *R. elegans* and of *wild* type *R. briggsae* as described by Nigon[12] and Nigon and Dougherty[14]—that is to say, temperatures from 23-25° C produce numerous abnormalities in meiosis with a resulting rise in the *andric index*.*

The eggs accumulate in the uteri of the mutant more than in those of the *wild* type animals—so much so, in fact, that, especially as a result of the reduced size, the hermaphrodites appear stuffed with eggs by the second day following sexual maturity. In Figure 9*A* it may be seen that there are only 5 eggs in the uteri of a *wild* type hermaphrodite, whereas in Figure 9*B* the uteri are filled irregularly with no less than 17 eggs. Apparently there is some abnormality in the laying process, which in

*A term introduced by Vandel[15] and signifying: $\frac{\text{no. of } \delta\,\delta}{\text{total no. of individuals}} \times 100$ for any given population.



NORMAL AND MUTANT NEMATODES

Figure 9

The mutant form of *Rhabditis briggsae* (*B*) is one quarter shorter and no less thick than the normal form (*A*). The photomicrographs show living adult hermaphrodites approximately one day after sexual maturity. Five cleaving eggs can be seen in the body of the normal inlividual (*A*). The mutant nematode is comparable, but contains at least seventeen eggs. Despite this retention of eggs it is much less fecund than the normal type.

turn is probably related to a change in cell number in the walls of the sexual apparatus. The adults cannot, in general, persist beyond the second day of maturity, at which, in cultures carried out at 16° C, most of the animals may be seen to have died. At 12° C, however, the hermaphrodites may live up to three days, rarely four, after sexual maturity. Fecundity is extremely low by comparison with the figures given for the *wild* type. Thus 63 isolated hermaphrodites produced a total of 881 descendants, averaging 14 per animal, whereas the *wild* type gave about 133 descendants per hermaphrodite.

The figures of Table I show that *micro* males are of equally reduced size. Moreover, the bursa presents by comparison with that of the *wild* type important differences (Figure 10*A* and *B*). The bursal papillae are more slender in the *micro* type. The bursa itself is foreshortened, thus losing the cardioid form characteristic of *R. briggsae* and *R. elegans*. Here again is a suggestion of a derangement in eutely.

Cytological examination carried out on hermaphrodites has shown that the number of spermatozoa present in the ovotestes is high; the low fecundity observed cannot therefore be attributed to an insufficiency in initial spermatogenesis. As in the *wild* type, diakinesis is marked by the appearance of six gemini, and maturation consists of the classic expulsion of two polar bodies. The mutation has thus not resulted in a change in the mode of reproduction of the species.

Production of the Mutation

The *micro* mutant appeared among the descendants of an hermaphrodite that had been submitted to a temperature of 25° C for 18 hours. This treatment permits the production of males as the result of irregularities occurring in meiosis.[12,14] Among a series of cul-

TABLE I. Comparison between the dimensions of *wild* type *R. briggsae* and the *micro* mutant.

	Hermaphrodites		Males	
	Wild type	*Micro*	*Wild* type	*Micro*
Total length	1.15-1.45mm	0.87-0.93mm	1.0-1.1mm	0.75-0.85mm
Width of body	70-90μ	65-75μ	45-55μ	
Length of esophagus	185-205μ	140-150μ*	170-180μ	150-160μ
Average position of vulva from anterior end	52%	54%		
Buccal cavity				
Length	12-14μ	10-12μ	11-13μ	11-13μ
Width	3.5-4.5μ	2.5-3.5μ	2.5-3.5μ	1.5-2.5μ
Eggs				
Length	52-58μ	51-57μ		
Width	28-30μ	30-36μ		
Number of eggs in uteri (up to second day after maturation)	2-5	9-17		
Length of spicules			32-38μ	32-34μ

*Measurement done without taking into account the S-shaped configuration of the esophagus.

TABLE II. Pedigree of certain of the earliest cultures of *Rhabditis briggsae* to contain the *micro* gene.*

Original culture	1st generation	2nd generation	3rd generation	4th generation	5th+ generations
Parent maintained at 25° C. for 18 hours		Isolated parents all of normal size. In progeny, appearance of some malformed or small sized animals			
			130 (W) 85	*139* to *142* (M) Whole progeny of small size (M)	M, constant
		104 (W) 37		*171* (W) 78W and 15M	
			136 (W) 19	*173* (W) 141W	
				174 (W) 17W and 3M	
				175 (W) 42W	
3 (W)	*81* (W)		*108* (W) 108	*156* (W) 100W	*206* (W) 90W
				176 (W) 10W and 8M	
			112 (W) 161	*177* (W) 34W and 6M	
				198 (W) 117W	
				199 (W) 25W	
				163 (W) 79W and 20M	
				164 (W) 24W and 6M	
		106 (W) 57	*113* (W) 48	*167* (W) 29W and 7M	
				168 (W) 122W and 26M	
				169 (W) 55W and 16M	
				170 (W) 61W and 22M	
			126 (W) 127	*143* (W) 62W	
			129 (W) 97	*138* (W) 40W	W, constant
			127 (W) 147	*149* (W) 54W	W, constant

*The *italic* figures correspond to the cultures as numbered in the original experimental series, each culture representing the progeny of a single hermaphrodite. The Roman figures represent the descendents obtained. W = *wild* type, M = *micro*; letters in parentheses indicate phenotype of single progenitor of each culture.

tures thus submitted to the action of heat and of which the descendants were followed, our attention was attracted by the fact that in two of these cultures we found animals that appeared malformed and of reduced vitality. Systematic examination of the lines involved soon showed us that an hereditary property was involved, of which the transmission seemed to be effected in a very regular manner. Table II furnishes the genealogy of the principal cultures that made up the first five generations studied.

The absence of *micro* in the descendants of several other cultures carried out under the same conditions and at the same time as culture *3* (Table II) and started with siblings of the parent hermaphrodite *3* obliges one to conclude that a mutation *de novo* must indeed have been involved, not earlier than in *3*. Examination of Table II shows, furthermore, that this mutation was produced at the latest in culture *81*, directly derived from the generation treated by heat, which included *3*. This agreement leads us to think that the elevated temperature to which culture *3* was submitted may have been the agent responsible for the appearance of the mutation; on the other hand there is as yet no evidence to refute the likelihood that it was merely a spontaneous mutation.

Disjunction of the Original Line

Animals of the *micro* type, once isolated, have produced as descendants hermaphrodites (and very occasional males) identical with themselves. For example, the several lines derived from *micro* animals selected from culture *130* (3rd generation) consistently gave this result (Table II).

On the other hand, hermaphrodites of the *wild* type derived from culture *3* did not give uniform progeny; certain of them produced only descendants identical with themselves, whereas others had progeny comprising both *micro* hermaphrodites and normal animals. This disjunction showed that parents of the latter type were in reality hybrid of nature. The fact that such hybrids could not be distinguished from homozygous *wild* type animals shows that the gene or genes producing *wild* type morphology behave as dominants over those determining the *micro* condition.

Among the descendents of hybrids *104* and *106*, we examined 33 hermaphrodites that were phenotypically of *wild* type. Among these, 13 gave only *wild* type descendants, and the *micro* type did not reappear in the lines that were derived from them; these animals thus appear to have been homozygous. Twenty others showed themselves to be hybrids. From 15 of these we counted the descendants, which comprised 550 hermaphrodites of the *wild* type and 150 of the *micro* type. In the following generation the same situation was manifested among the various phenotypically *wild* type animals—that is, certain of them only produced *wild* type descendants and thus were homozygous; others furnished both *wild* type and *micro* individuals, thus proving their heterozygous nature.

TABLE III. Descendants obtained by crossing *wild* type ♂♂ with *micro* Hermaphrodite of *R. briggsae*.

No. of Culture	*Micro* Her.	*Micro* ♂♂	*Wild* type ♂♂	*Wild* type Her.	Total
57	19	1	1	1	22
54	18	..	3	2	23
2C	3	..	2	1	6
3C	6		1		7

Crosses of *Wild* Type and *Micro*

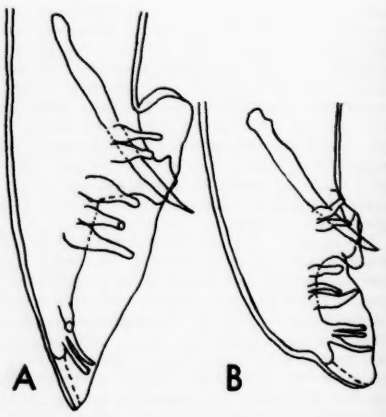
The reduced fertility and low vitality of *micro* hermaphrodites has rendered rather difficult the realization of crosses between *wild* type and *micro*. We have, however, obtained several positive results in pairing *micro* hermaphrodites with *wild* type males. Among 13 attempts in France and 12 in California, 2 and 4 respectively met with success, these manifesting themselves by the appearance of *wild* type hermaphrodites in the descendants, among which we also observed *wild* type males in all but one of the latter. The descendants obtained in most of these experiments are grouped in Table III.

Among the animals derived from cultures *54* and *57* (done in France) 8 *micro* hermaphrodites furnished 99 hermaphroditic descendants, all *micro*. As in the self-fertilized original line, the *micro* phenotype thus was associated with homozygous animals. By contrast the two *wild* type hermaphrodites gave a total of 195 *wild* type descendants and 74 *micro* descendants. Among the *wild* type animals of the second generation 17 were examined. Three of these were homozygous and produced only *wild* type descendants; 14 were hybrids, giving a total of 775 *wild* type hermaphrodites and 215 *micro* hermaphrodites. Descendants of cultures *2C* and *3C* (done in California) were not counted after the F_1 generation, but gave similar results as judged by general inspection of the slides. (The other two California cultures were inspected, but not counted).

The utilization of three males of the *wild* type issuing from the *wild* type and *micro* cross permitted us to obtain a certain number of *micro* males and hermaphrodites, both by crossing them with *micro* hermaphrodites and by mating them with heterozygous hermaphrodites of the *wild* type; it is thus necessary to conclude that the *micro* gene is not sex-linked. Numerical examination of the disjunctions obtained in the descendants of heterozygotes of the *wild* type leads us to think that the appearance of the *micro* form was the result of a single-factor mutation. In effect, in grouping the figures obtained in the original self-fertilized line and as a result of the experiments on crossing we see that 31 heterozygous hermaphrodites furnished a total of 1959 descendants—1520 *wild* type, 439 *micro*. Among

the descendants of phenotypic *wild* type, 50 were examined. Sixteen of these were shown to be homozygous, and thus 34 were heterozygous. This latter proportion (*wild* type heterozygotes/*wild* type homozygotes) corresponds much more than the first (phenotypic *wild* type/*micro*) to a simple single-factor disjunction. In other words the single-factor hypothesis would demand that one have 3 *wild* type descendants for 1 *micro*; or, in an observed total of 1959 individuals, 1469 should have been *wild* type and 490 *micro* in morphology. The deviation from the expected ratio is statistically significant. Among the *wild* type animals 2 heterozygotes for 1 homozygote would be expected—a figure effectively obtained. The insufficiency of *micro* descendants by comparison with theoretical predictions deriving from a single-factor hypothesis may be explained, in all probability, by a reduced vitality of these animals, which no doubt results in a significant lethality.

In addition to experiments just described, on the inheritance of the *micro* gene within *R. briggsae*, we also attempted, as described in detail elsewhere[14] to cross heterozygous males of this species with hermaphrodites of *R. elegans*. The failure of the gene to manifest itself phenotypically in the F_0 from this supposed cross was additional (although, of itself, not conclusive) evidence of the intersterility of these two closely allied species.



WILD TYPE AND MUTANT BURSAE

Figure 10

The wild type and the mutant forms are specifically alike in many respects. There are recognizable morphological differences in mutants. Here are shown camera lucida drawings of the bursae of a preserved specimen of wild type (*A*) of the mutant (*B*), approximately 1000 ×.

Discussion

The discovery of a morphological mutant in a species of *Rhabditis* constitutes an encouragement for continued studies on the genetics of these animals. It proves that, even for animals of which the morphology appears very monotonous and hence possibly not susceptible of drastic change without intervening lethality, viability of easily detected mutant forms may be sufficient to permit genetic studies.

Examination of the *micro* mutant of *R. briggsae* gives us, morever, a supplementary proof of the rather arbitrary character of specific criteria widely used for such forms. It appears evident that this mutant, if discovered in nature, would have been considered as type of a new species, without apparent connection with the species from which it had issued. If one adds this observation to those that we have previously made[14] on the impossibility of effecting crosses between *R. briggsae* and *R. elegans*, which are perhaps morphologically more similar in general appearance than are the *wild* type and mutant of *R. briggsae*, then we are obliged to remark that, for these animals, of which the organization is very simple, the usual criteria of species may not apply very well in some cases. In this connection it may be further remarked that such examples will probably multiply in measure with genetic studies carried out.

The apparent derangement of eutely in the *micro* mutant of *R. briggsae* suggests interesting possibilities for investigating something of the underlying nature of cellular constancy among the aschelminths. It will be highly desirable to carry out an exact cytological study of both the *wild* type and *micro*—specifically to make a census of somatic nuclei in the two strains so that the mutation may be described in terms of nuclear number and arrangement.

Quite apart from its theoretical significance such a mutant as *micro* has a practical importance for the methodology of genetic studies on *R. briggsae* and other species with similar sexual patterns. Already, as mentioned, it has been

used[14] as an additional test of the cross-sterility of *R. briggsae* and *R. elegans;* its failure to manifest itself phenotypically in the F_2 derived from a P "cross" of *R. elegans* hermaphrodite × *R. briggsae* ♂ ♂ (heterozygous for the *micro* gene) was strong collateral evidence that the cross was not taking place.

As new mutants are discovered it will become important to test for linkages. The phenotype of *micro* should make it useful as a chromosome marker, at least until more fertile mutants are discovered. To be sure, such mutants are highly desirable and will be sought; but even in the absence of such forms, the striking phenotypic difference between *micro* and the *wild* type will, in general, permit the rapid selection of the desired progeny, especially in distinguishing those arising by self-fertilization from those by cross fertilization in cases where *micro* hermaphrodites are used.

A number of workers of a decade or more ago suggested that free-living nematodes might prove of value for genetic studies.[1,2] Our recent investigations tend, we feel, to support their prediction. In the last two years it has become possible to say: 1) that there are available relatively simple techniques that permit rapid study of large genetic series and the sex-cell cytology of these forms;[12] 2) that they are mutable under laboratory conditions (the present work); and 3) that they can be cultivated under axenic conditions.[5,6,7] Morphological and cyto- genetic work is now realizable, and the outlook for biochemical genetic work appears good. It seems thereby justified to hold an optimistic view toward the potential role of these organisms in fundamental genetic investigation.

Summary

1. A morphological mutant of the self-fertilizing, hermaphroditic, free-living nematode species *Rhabditis briggsae* Dougherty and Nigon, 1949, is described in detail—the first to be reported in the phylum Nematoda.

2. It is designated *micro* and affects the gross appearance of the homozygous individuals by a general reduction in size, impairment of the egg-laying mechanism so that the ova are laid so slowly that they accumulate and kill the hermaphroditic parent, and alteration in the structure of the male copulatory bursa.

3. The mutation appeared after heat treatment among descendants of one of a series of isolated hermaphrodites kept at a temperature of 25° C for 18 hours during the time of sexual maturation. It is not yet possible to state whether or not a causal mechanism between heat and mutation may exist in these forms. The inheritance of the *micro* gene is shown to follow a single-factor pattern and to be recessive and not sex-linked.

4. Experiments are described in which *micro* hermaphrodites have been successfully outcrossed with *wild* type males. The self-fertilized progeny of the *micro* parent can be readily distinguished from the cross-fertilized hybrid progeny by the mutant phenotype of the former vs. the *wild* phenotype of the latter.

5. The theoretical consequences of the production of this mutant are discussed in relation to the general taxonomy of the group, to the phenomenon of eutely (cell-constancy), to the practical usefulness of the *micro* gene as a chromosome marker and a test of cross-fertilization in linkage and other genetic experiments, and to the general potential importance of free-living nematodes in genetic research.

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*Incorrectly cited by Nigon[11] as "A mutant type of *Rhabditis elegans brevis.*"

EVOLUTION UP TO DATE

A Review

FUTURE historians of science may not wholly agree with Whitehead's dictum (quoted by Jepsen in this symposium*) that the last twenty years of the nineteenth century were one of the dullest stages of thought since the First Crusade. They will, nevertheless, note that this was a period when most work on evolutionary theory was destructive and little apparent progress was made in understanding problems stated but not fully solved by Darwin. This was followed in the first generation of our own century by apathy toward Darwinian ideas and enthusiasm for the rising science of genetics, which to some seemed to make discussion of such topics as adaptation and natural selection not only dull but also unnecessary.

Now we are witnessing a remarkable revival of interest in evolution. The most active aspect of genetics is precisely evolutionary genetics, and it does not supplant but becomes integrated with the great flow of thought started by Darwin. Weaknesses and difficulties of earlier theories are being largely overcome. The most hopeful sign of all is that this movement has permeated and revivified almost all branches of biological science. In the study of evolution all biologists are developing a common basis and mutual understanding. Bickering and miscomprehension are being replaced by unexpectedly wide agreement on the essentials of evolutionary theory, outside the ranks of politically ideological Michurinism and of the increasingly non-vital schools of vitalism. The excellent symposium here reviewed is both added evidence of this movement and an outstanding contribution to its progress.

Two geneticists, a paleontologist, a botanist, and a zoologist, all among the most eminent students in their fields, here discuss the problem of adaptation from their diverse points of view. All agree that adaptation is the main key to the orderly sequences of evolution, and all agree in essentials as to the mechanism by which adaptation is achieved, a mechanism in which basic (although not the only) elements are genetic mutation and natural selection.

Darwinian Adaptation Vindicated

Darwin emphasized the crucial role of adaptation and he proposed natural selection as the main cause of adaptation. To this extent, then, the modern synthesis is a vindication and triumph for Darwinism, as Muller's contribution to this symposium makes quite clear. Muller also points out how much wider is the agreement with Darwin than might casually be gathered from the current literature. For instance, Darwin was aware of relationships between population size and the action of selection, commonly viewed as a recent discovery of the population geneticists. Of course, the modern students have made knowledge of this relationship more extensive and more precise. Over a large part of the field, modern concepts do thus represent extension and precision rather than essential change of Darwin's ideas. Yet some of Darwin's ideas have been wholly rejected, and real knowledge of the one whole aspect of the interaction of organism and environment is in effect entirely post-Darwinian. This aspect involves genetic factors, and especially, as Muller lists them, these: (1) the fact that the hereditary material is particulate, (2) the rules of transmission of these particles, (3) information on such phenotypic interrelations as dominance, pleiotropy, and multiple-factor cases, and (4) evidence on the quantum character of changes in inheritance and data on the frequency of such changes.

*Natural Selection and Adaptation. *Proc. Amer. Phil. Soc.*, vol. 93, no. 6, pp. 459-519, Dec. 1949. H. J. Muller, The Darwinian and Modern Conceptions of Natural Selection. Sewall Wright, Population Structure in Evolution. Glenn L. Jepsen, Selection, "Orthogenesis," and the Fossil Record. G. Ledyard Stebbins, Jr., Reality and Efficacy of Selection in Plants. Ernst Mayr, Speciation and Selection.

Muller's lack of complete agreement with some of his colleagues points up the continued existence of unsolved problems, important and yet mainly matters of detail. He questions the usual assumption that recessivity is valuable in providing a source of hidden variability, and he mentions the growing evidence that dominance and recessivity are not simple alternatives. He also strongly opposes the view that natural selection may directly favor intersterility and so be effective in the origin of isolating mechanisms. In taking a somewhat narrower definition of selection and yet emphasizing selection as an inclusive explanation within its scope, Muller may be more strictly Darwinian, perhaps also closer to neo-Darwinism strictly speaking, than the apparent consensus of modern students.

The Tools of Speciation

Muller points out that among the respects in which we have gone far beyond Darwin is the quantitative treatment of population dynamics and of the complex interrelationships involved in adaptation and in evolution more generally. Here the name of Wright at once rises to mind, and Wright, himself, has contributed to the symposium a brief paper exceptionally broad in scope and crystalline in logical clarity. His mathematical telescoping of argument has made most of Wright's work at first hand difficult and esoteric for the average student, but here the exposition is mainly in the vernacular and the reasoning is verbal except for one formula readily skipped by the uninitiated. In five outlines with accompanying glosses, he has summarized practically the whole of the evolutionary process as he sees it, from the origin of life to that of any given species.

Without attempt to condense further so concise a summary, its contents are glimpsed from the titles of the outlines: (1) Major steps in evolution [from the gene to species of multicellular individuals], (2) Modes of change of gene frequency (q), (3) Modes of transformation of species [i.e., of their monophyletic evolutionary change; Gregory and others have given "transformation" a different meaning], (4) Modes of origin of species [i.e., mainly of speciation in the usual sense], and (5) The evolutionary cycle.

Perhaps the most interesting elements in this treatment, so stimulating and suggestive throughout, are the attention given to evolution without speciation, "transformation" in Wright's sense, and to broadly historical features of evolution, aspects seldom stressed by geneticists or neontologists. The reader is given an appetite for a fuller discussion of these historical aspects of evolution. Criticisms on this extension of principles from a point in time to the time scale of earth history would bear mainly on uncertainty or incompleteness that may be inherent in brevity of presentation, only.

The Paleontological View

It is the paleontologist who customarily deals with major evolutionary events and long time sequences, and a paleontologist also here has his say on the general topic. Jepsen's treatment is mostly by citation and quotation of pertinent literature, soundly evaluated and often wittily annotated. One of his important achievements is demonstration that appeals to paleontology for support of diverse evolutionary theories have developed a sort of folklore among the non-paleontologists. Paleontology has sometimes been pictured as a hot-bed of Lamarckism, of orthogenetic vitalism, and of all sorts of anti-Darwinian or, at least, anti-selection heresies. There have been some grounds for this view, but since 1859 there have always been many paleontologists whose evaluation of selection has been about that now reached by the geneticists, and certainly this position is overwhelmingly favored by paleontologists today.

Orthogenesis, in a somewhat metaphysical sense, has long been credited to the paleontologists as their peculiar property. In fact, as Jepsen shows, the term, itself, and most of the highly diverse concepts intended by the term "or-

thogenesis" were developed by neontol- and most of the supporters of the more metaphysical of these concepts have been neontologists. More neontologists than paleontologists have supposed that paleontology warrants such views. Jepsen aligns himself with the great majority of modern paleontologists in concluding that such real phenomena as might be called orthogentic are the results of orthoselection.

Jepsen provides an unusually good, new, objective example of large-scale selection from the fossil record: ecological replacement of one mammalian order (Multituberculata) by another (Rodentia) in late Paleocene to early Eocene by what seems clearly to have been inter-group selection. During the sterile period of the late 1800's and early 1900's, one of the most cutting criticisms of Darwinian theory was directed at the supposed absence of concrete and verifiable examples of natural selection effectively in action. Jepsen's is an excellent historical example, and Stebbins contributes to the symposium convincing examples from experimental, ecological, and (botanical) comparative anatomical studies.

Although Stebbins' paper is no less able or important than the others, further notice of it is omitted here. It is based on material expounded in a book announced for early publication, and critical notice may profitably and fairly await the full text.

Selection and the Origin of Species

Finally, Mayr has related selection to the realities of evolution at the basic level where systematists are most likely to work. Criticisms of selection have also concentrated on this point, maintaining that selection might be effective within species, or (with other critics) between species, but that the crucial events of origin of species were not adaptively oriented or selectively induced. Such views are effectively demolished by Mayr, quietly and briefly. Part of the trouble arose from a literally unrealistic (that is, philosophically idealistic) concept of the species, and part of speciation. Local populations are the ancestors of species. The populations are locally adapted and the differences between them are in the main adaptive. Further adaptive differentiation between them is a major element in their separation as species. Selection is instrumental in their genetic isolation following this differentiation. (Here there is a difference of interpretation from Muller, as above, that needs further discussion.)

All in all, this is a major contribution to the literature of evolutionary theory. Where else will you find such an authoritative, fresh, and well-rounded discussion of essential problems of life for seventy-five cents?

G. G. Simpson

American Museum of Natural History

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"THE MENTOR" AND THE ATOM

SO THEY SLAM THE DOOR IN YO FACE—ON I KNOWS THEY UP TO SOME SORT OF PRIVACY.
THEY IS UP THERE EATIN' GOODIES AN' WON'T GIVE ME THE BORRY OF A MEASLE CUP OF SUGAR
NOW DE TURTLE YOU SEES A GEE-RANIUM PLANT AN' A LI'L BABY YEW TREE --- (IS THE DOOR LOCKED?) S'POSE I CROSSES THESE KIDS -- WHAT THEN?
I KNOWS! I KNOWS! YOU CROSSES 'EM AN' YOU GITS TO THE OTHER SIDE.
HOW EEE-DICULOST! IF YOU CROSS THESE, YOU GITS A YEW-RANIUM BUSH!
NNNPH
WELL, DE LYSINE! WE BEEN WAITIN' HALF A HOUR--- MEBBE IF WE CROSSES OUR FINGERS, TOO?

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